Can the Genetic Antagonisms of Callipyge Lamb be Overcome?[1]

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[1]Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of other products that may also be suitable. We would like to thank Noelle Cockett, Kreg Leymaster, and Morse Solomon for providing us with information necessary to assimilate this manuscript.

Introduction

The ultimate goal of livestock and meat science research should be to identify the most efficient means to produce wholesome, nutritious, highly palatable products that fit the needs of consumers. In the United States, *per capita* consumption of red meat has steadily declined over the last thirty years due to a failure of the meat industry to provide economical products that meet all of the needs of the modern consumer. Many factors, most of which are beyond the scope of the present discussion, have contributed to the failure of the red meat industry to keep up with changing needs and desires of consumers. One factor that has limited the red meat industry's ability to improve product desirability is genetic antagonisms. The present discussion centers on the genetic antagonism between carcass composition and meat tenderness associated with the callipyge condition in lamb. Information gained from studying this antagonism in lamb should help researchers to chart a course for overcoming similar antagonisms, including those not yet discovered, in species of greater economic importance. Given the high level of conserved genomic synteny among ovine and bovine, this information should be readily applicable to cattle.

Inheritance of Callipyge

To fully understand the potential effects of the callipyge phenotype on the lamb industry, one must have an understanding of the mode of inheritance of the callipyge condition. Inheritance of the callipyge condition has been described as polar overdominance (Cockett et al., 1996) because only heterozygous

individuals that have inherited the mutant callipyge allele from their sire and the normal allele from their dam express the callipyge phenotype.

Although the inheritance of the callipyge condition is complex, it would still be rather easy to implement mating systems to maximize the production of callipyge lambs. Production of callipyge lambs would be maximized by mating homozygous callipyge rams, which would appear phenotypically normal, with homozygous normal ewes. Until recently, the only method to identify homozygous callipyge sires for such a mating program was to progeny test those rams by mating them to a large number of homozygous normal ewes and evaluating the phenotype of offspring. Since the gene responsible for the callipyge condition has been localized to ovine chromosome 18 (Cockett et al., 1994) and its position refined (Freking et al., 1998a), it is now possible to use marker-assisted selection to identify homozygous callipyge animals. Thus, flocks of homozygous callipyge animals could be established to produce homozygous callipyge rams for a terminal mating system. The most logical approach would be to introgress the mutant callipyge allele into a terminal (meat type) sire line. When homozygous callipyge rams produced from such a line are mated to normal, maternal line ewes, 100% of the progeny would be expected to express the callipyge phenotype.

Characterization of Callipyge

For most traits of economic importance to the lamb industry, the effect of the callipyge condition has been well documented.

Compared with normal lambs of similar breed type, lambs expressing the callipyge phenotype have similar birth weights, weaning weights, and post-weaning growth rates (Jackson et al., 1997a). The incidence and severity of dystocia are similar for normal and callipyge lambs. Callipyge lambs do not appear phenotypically different from their normal siblings until approximately 2 to 12 wk of age.

Grain-fed Market Lambs

Dressing percentage is 3 to 5 percentage points higher for callipyge carcasses than normal carcasses (Koohmaraie et al., 1995b; Jackson et al., 1997b). The increased dressing percentage of callipyge results from a combination of a tendency for reduced weights of most dress-off items (internal organs, perinephric fat, and pelt but not head or blood) and a tendency for callipyge carcasses to be heavier (Koohmaraie et al., 1995b).

Callipyge lambs produce carcasses that are approximately 30% more muscular and that have 30% less fat (Koohmaraie et al., 1995b; Jackson et al., 1997b). The callipyge phenotype reduces subcutaneous, intermuscular, intramuscular, and perinephric fatness. The combined effects of the callipyge condition on dressing percentage, muscularity, and fatness result in dramatic improvements in yields (Table 1; Jackson et al., 1997b). Depending on the retail fabrication style, trim level, and method of expressing yields, the improvement in yield associated with the callipyge condition ranged from 7.7% (bone-in, untrimmed retail product as percentage of carcass weight) to 32.6%

(boneless, completely trimmed retail product as percentage of live weight).

The increased muscling associated with the callipyge phenotype is not uniform across all muscles (Table 2). Weights of most major muscles are increased by the callipyge condition; however, the effect is not uniform and, in fact, weights of some shoulder muscles are not affected by the callipyge condition (Koohmaraie et al., 1995b; Jackson et al., 1997c).

Why are callipyge more muscular?

Knowing that callipyge lambs were more muscular than their siblings, we set out to determine the mechanisms responsible for the increased muscularity of callipyge.

Hyperplasia or hypertrophy?

The first question that we attempted to answer was if the increased muscularity of callipyge was due to hyperplasia or hypertrophy. Before we initiated our experiments to determine if the increased muscularity of callipyge was due to hyperplasia or hypertrophy, we already had a preconceived notion that the increased muscularity of callipyge was due to hypertrophy because of observations that callipyge lambs did not appear more muscular at birth. That is, if callipyge was a result of increased hyperplasia, which occurs mostly prenatally, we would have expected callipyge lambs to be more muscular at birth.

We (Koohmaraie et al., 1995b) observed similar estimates of apparent muscle fiber number for normal and callipyge semitendinosus suggesting that hyperplasia was not responsible for the increased muscularity of callipyge lambs. Furthermore,

we (Koohmaraie et al., 1995b) observed increased cross sectional areas of α-red and α-white muscle fibers and a higher proportion of α-white muscle fibers for callipyge longissimus and semitendinosus. The combined changes in size of α-red and α-white muscle fibers and the shift in muscle fiber types resulted in overall estimates of longissimus and semitendinosus cross sectional muscle fiber area being 48 and 62% higher for callipyge (Koohmaraie et al., 1995b). Collectively, these findings support the hypothesis that the increased muscularity of callipyge lambs is caused by hypertrophy and not hyperplasia.

Increased protein synthesis or decreased protein degradation?

Having established that the increased muscularity of callipyge lambs is caused by hypertrophy we next attempted to determine if the hypertrophy was a result of increased protein synthesis or decreased protein degradation. In market lambs, we (Koohmaraie et al., 1995b) observed that the callipyge phenotype increased longissimus and semitendinosus DNA, RNA, and protein content by approximately 30%, suggesting a greater capacity of callipyge muscles to synthesize and maintain protein. Also, we observed that calpastatin activity was higher for most skeletal muscles from callipyge, suggesting that protein degradation may be reduced in callipyge skeletal muscles via calpastatin-induced down regulation of calpain. In support of that hypothesis, we showed that the relative effect of the callipyge condition on weights of the various muscles was proportional (R^2 = .91) to the relative effect of the callipyge condition on calpastatin activity (Figure 1).

To establish if there was a direct effect of the callipyge condition on protein synthesis or degradation, we (Lorenzen et al., 1997) measured protein accretion, synthesis, and degradation rates in muscles and tissues of 8 wk old lambs. Both the fractional rate of protein synthesis and the fractional rate of protein degradation were lower for callipyge longissimus and biceps femoris. Additionally, for infraspinatus and supraspinatus, which are not hypertrophied by the callipyge condition, neither the fractional rate of protein synthesis nor the fractional rate of protein degradation was affected by callipyge phenotype (Figure 2).

Collectively, these findings support the hypothesis that the increased muscle hypertrophy of callipyge lambs is caused by decreased protein degradation. But, present data do not permit exclusion of a role of protein synthesis in causing callipyge-induced muscle hypertrophy before 5 wk of age.

The Antagonism

Because the callipyge phenotype greatly increases (19 to 126%) calpastatin activity for most major muscles, the rate of postmortem proteolysis is dramatically reduced for those callipyge muscles and, thus, those callipyge muscles are much tougher than normal muscles even after extensive aging (Koohmaraie et al., 1995b; Shackelford et al., 1997; Freking et al., 1998b). The negative effect of the callipyge condition on meat tenderness appears to be particularly large for longissimus (Shackelford et al., 1997). In fact, oven roasting eliminates the toughness of callipyge lamb legs (Shackelford et al., 1997).

Therefore, most efforts to insure the tenderness of callipyge meat have focused on longissimus.

Mitigating the Callipyge Antagonism Genetically

It appears that there is a direct association between the effects of the callipyge condition on carcass muscularity and meat tenderness. Apparently, by increasing calpastatin activity, the callipyge condition results in decreased rates of antemortem and postmortem protein degradation. Given that calpastatin appears to play an essential role in the increased muscularity of callipyge, it appears that any attempt to improve the tenderness of callipyge by selecting against calpastatin would result in a loss of both the positive and negative aspects of callipyge.

It might be possible to mitigate the negative effects of the callipyge condition on meat tenderness by selecting for genetic combinations that are moderate to the present callipyge condition. That is, the optimal genetic combination might be one that results in a modest increase in calpastatin activity, a modest decrease in fractional breakdown rate, a modest increase in carcass muscularity, and a modest decrease in meat tenderness.

<u>Carwell Locus for Lamb Muscling</u>

Recently, research in Australia suggested that a locus for extreme muscling was segregating in some families of Australian Polled Dorset (Banks, 1997). The Carwell condition has been reported (Nicoli et al., 1998) to result in a smaller increase in longissimus area than has been reported for the callipyge condition (Koohmaraie et al., 1995b; Jackson et al., 1997b).

Data are not yet available for the effect of the Carwell condition on meat tenderness.

The Carwell condition has been linked to the region of the ovine genome that has been shown to contain the callipyge locus (Cockett et al., 1996; Freking et al., 1998a). However, phenotypic data indicate that this condition is not as extreme as the callipyge condition. It is possible that a different allelic form of the same gene as the one that causes the callipyge condition causes the Carwell condition. The Carwell condition appears to show the same type of polar overdominant inheritance as Cockett et al. (1996) described for the callipyge phenotype. As with the callipyge phenotype, it appears that only heterozygous individuals that have inherited the mutant allele from their sire and the normal allele from their dam express the Carwell phenotype.

Mitigating the Callipyge Antagonism Environmentally

Numerous approaches to overcoming the inadequate tenderness of callipyge have been examined (Table 3). The first approach explored for tenderizing callipyge was extended postmortem aging (Koohmaraie et al., 1995b). Koohmaraie et al. (1995b) reported that aging callipyge longissimus from 1 to 21 days resulted in a 25% ($P < .001$) reduction in Warner-Bratzler shear force. However, callipyge longissimus aged 21 days tended ($P = .12$) to be less tender (higher Warner-Bratzler shear force) than normal longissimus at 1 day postmortem. Thus, it appeared that aging alone would not serve to overcome the inadequate tenderness of callipyge. This was confirmed by Busboom et al. (1997) who

showed that Warner-Bratzler shear values were higher for callipyge loin chops aged 80 days than normal loin chops aged 14 days.

Calcium-activated tenderization has been shown to be an effective method to increase the rate of postmortem proteolysis in beef and lamb (Koohmaraie et al., 1993). Therefore, there has been much interest in the use of calcium-activated tenderization as a method to overcome the inadequate tenderness of callipyge. All of the studies reviewed showed that calcium-activated tenderization resulted in improved tenderness of callipyge longissimus (Koohmaraie et al., 1995a; Leckie et al., 1997; Duckett et al., 1998). However, there was disagreement among studies in the level of effect achieved with calcium-activated tenderization. Whereas Koohmaraie et al. (1995a, 1998) reported that calcium-injected callipyge longissimus had Warner-Bratzler shear values 41 to 113% higher than non-injected normal longissimus, Leckie et al. (1997) reported that callipyge longissimus injected with calcium chloride and aged until 14 or 28 days postmortem had Warner-Bratzler shear values similar to non-injected normal longissimus aged until 14 days postmortem.

Electrical-stimulation is a rather simple tenderization technology that could be easily utilized by lamb packers; however, high-voltage, high-frequency electrical stimulation has little or no effect on callipyge longissimus Warner-Bratzler shear force (Leckie et al., 1997; Shackelford et al., 1998).

Frozen storage has been shown to result in loss of calpastatin activity (Koohmaraie, 1990) and, thus, if beef

samples are frozen and held for approximately 30 d, thawed, and then aged, the rate of proteolysis may be slightly increased (Crouse and Koohmaraie, 1990). Therefore, there has been interest in using freezing as a method to decrease the level of calpastatin activity in callipyge muscles. Leckie et al. (1997) reported that freezing of callipyge chops for 4 days before thawing and aging did not affect longissimus Warner-Bratzler shear force. However, Duckett et al. (1998) reported that when callipyge chops were frozen at 24 h postmortem for 6 weeks and subsequently thawed and aged for 24 days, callipyge chops had longissimus Warner-Bratzler shear force values similar to normal longissimus chops.

Koohmaraie et al. (1998) showed that callipyge longissimus tenderness could be improved by limiting the extent of postmortem sarcomere shortening. At approximately 17 minutes postmortem, carcasses were submersed in liquid nitrogen for a period of 15 minutes. This resulted in longissimus temperatures of approximately –2.3 and –14.5°C at 35 and 62 min after slaughter, respectively. This process did not completely inhibit rigor shortening. However, as compared with conventionally-chilled carcasses, carcasses frozen in liquid nitrogen had increased longissimus sarcomere length (1.99 vs 1.63 μm). That increase in sarcomere length translated into a reduction in longissimus Warner-Bratzler shear force of 32 and 30% at 7 and 14 days postmortem, respectively. Nonetheless, those shear values were still 51 and 63% higher than normal longissimus at 7 and 14 days postmortem, respectively. To consistently produce loin chops

with Warner-Bratzler shear values less than 5 kg, Koohmaraie et al. (1998) found that it was necessary to combine liquid nitrogen freezing, calcium-activated tenderization, and aging in a multiple hurdle approach (Figure 3).

Another approach to tenderizing callipyge is the Hydrodyne process, which functions by mechanical disruption of the muscle ultrastructure (Solomon et al., 1997). Hydrodyne appears to be an effective method of instantaneous tenderization of callipyge (Leckie et al., 1997).

Economics

As lamb producers, processors, and marketers make plans to strengthen consumer demand for lamb, they will be forced to decide whether or not to utilize callipyge genetics. If callipyge lambs are produced, then packers, processors and retailers will have to decide whether to tenderize callipyge lamb before passing that product down the marketing chain to the consumer. Ultimately, the consumer will decide to what extent the desirable characteristics of callipyge offset its negative effects on meat tenderness.

We have summarized how each segment of the marketing chain would be affected if callipyge genetics were introgressed into a terminal sire line (Table 4). Because the callipyge phenotype does not affect survivability, dystocia, or growth rate, production of callipyge lambs would have little effect on the breeding segment of the industry. However, commercial lamb producers may have to pay a premium to procure homozygous callipyge rams. Lamb feeders would benefit from the improved

feed efficiency of callipyge. Packers would reap the benefits of the effect of the callipyge phenotype on dressing percentage; however, packers may have to bear the cost of tenderizing callipyge. Retailers would reap the benefits of the effect of the callipyge phenotype on cutting yields. Because of increased muscle size and the higher percentage of lean in callipyge cuts, consumers would likely find callipyge cuts to be more attractive than typical lamb cuts. This would likely result in an initial increase in the volume of lamb sold by retailers. However, consumers may react negatively to the toughness of callipyge. Therefore, introduction of callipyge lamb to the marketplace might adversely affect long-term trends in lamb consumption unless callipyge was tenderized sufficiently.

It is likely that the packing segment will have to bear the cost of tenderizing callipyge. Thus, we have approximated the potential economic benefits of callipyge to the packing segment (Table 5). In our calculations, we assumed that packers buy lambs on a live weight basis and sell three-way boxed lamb. With this approach, the only one of the advantages of callipyge that would be captured by the packing segment would be dressing percentage. If a packer were to fabricate carcasses into trimmed subprimals, the callipyge advantage would be greater (Table 1). We conservatively estimate that the multiple hurdle tenderization approach described by Koohmaraie et al. (1998) would cost $5.00/carcass. The economic advantage associated with the higher dressing percentage of callipyge is likely great enough to offset the cost of tenderization.

Comparison to Double Muscling in Cattle

Double muscling in cattle, which is caused by mutations in the myostatin gene (Smith et al., 1997, 1998), and the callipyge condition in lamb are similar in that both conditions increase carcass muscularity and decrease carcass fatness. However, there are several distinct differences between double muscling in cattle and the callipyge condition in lamb (Table 6). The increased muscling associated with double muscling is primarily a result of hyperplasia, whereas the increased muscling associated with callipyge is a result of hypertrophy. Because double muscling is a result of hyperplasia, which occurs primarily prenatally, double muscling increases birth weight and the incidence and severity dystocia. Because callipyge is a result of hypertrophy, which occurs primarily postnatally, callipyge does not affect birth weight or the incidence and severity of dystocia.

Because double muscling increases the incidence and severity of dystocia, cow-calf producers have been reluctant to produce double-muscled calves. However, when intermediate double-muscled calves are produced by mating double-muscled bulls to normal, mature cows, the effect on birth weight and dystocia is small (Casas et al., 1998). Thus, intermediate double-muscled calves could be produced in a roto-terminal mating system without deleterious effects on calving.

Whereas the callipyge phenotype has deleterious effects on longissimus tenderness (Koohmaraie et al., 1995b), the

intermediate double muscling phenotype does not effect longissimus tenderness (Casas et al., 1998).

Avoiding Antagonisms

The callipyge condition in lamb and double muscling in cattle represent two different methods to increase carcass muscularity and decrease carcass fatness. However, both methods result in improvement in carcass composition at the expense of other traits. Given the link between proteolysis rates in antemortem and postmortem muscle, it would appear that selection for decreased protein degradation would almost certainly have negative consequences on meat tenderness. On the other hand, selecting for increased hyperplasia will almost certainly increase the incidence and severity of dystocia in cattle. However, the intermediate double muscling phenotype only has minor effects on birth weight and the incidence and severity of dystocia when intermediate double muscled calves are produced from mature, normal phenotype cows. The effect of selection for increased hyperplasia on dystocia may be less in litter-bearing species. Muscle growth could be increased by selecting for increased protein synthesis. However, selection for increased protein synthesis may result in decreased efficiency of utilization of protein as it has been shown that exogenous growth hormone results in increased rates of both protein synthesis and protein degradation (Tomas, et al., 1992). It would appear that growth hormone has the opposite effect on protein turnover as the callipyge condition.

Until marker-assisted selection schemes can be developed to circumvent genetic antagonisms, it appears that selection for any trait should be conducted with attention to the effects of that selection on other traits. Ultimately, the best alleles for meat production may be those that have moderate effects on production traits, carcass composition, and meat tenderness rather than the extreme effects induced by callipyge and myostatin.

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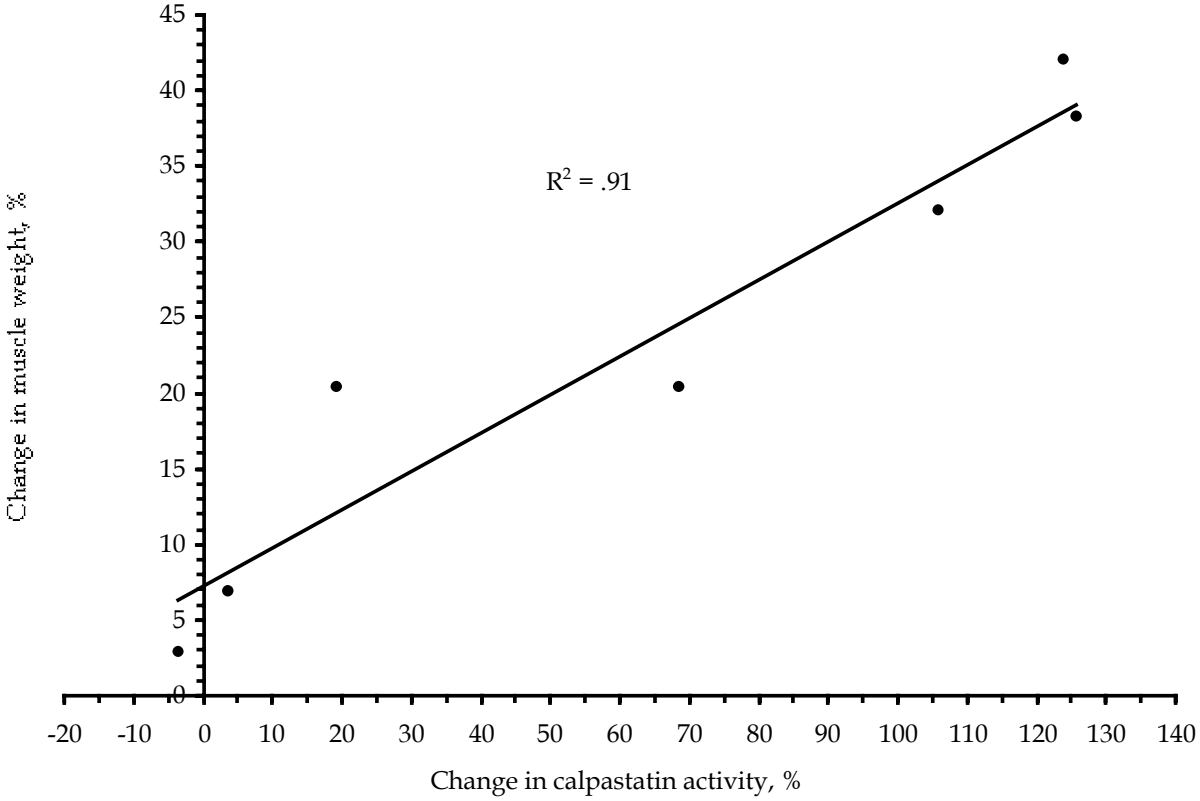

Figure 1. Relationship between the effect of the callipyge phenotype on calpastatin activity of various muscles and its effect on muscle weight. Adapted from Koohmaraie et al. (1995).

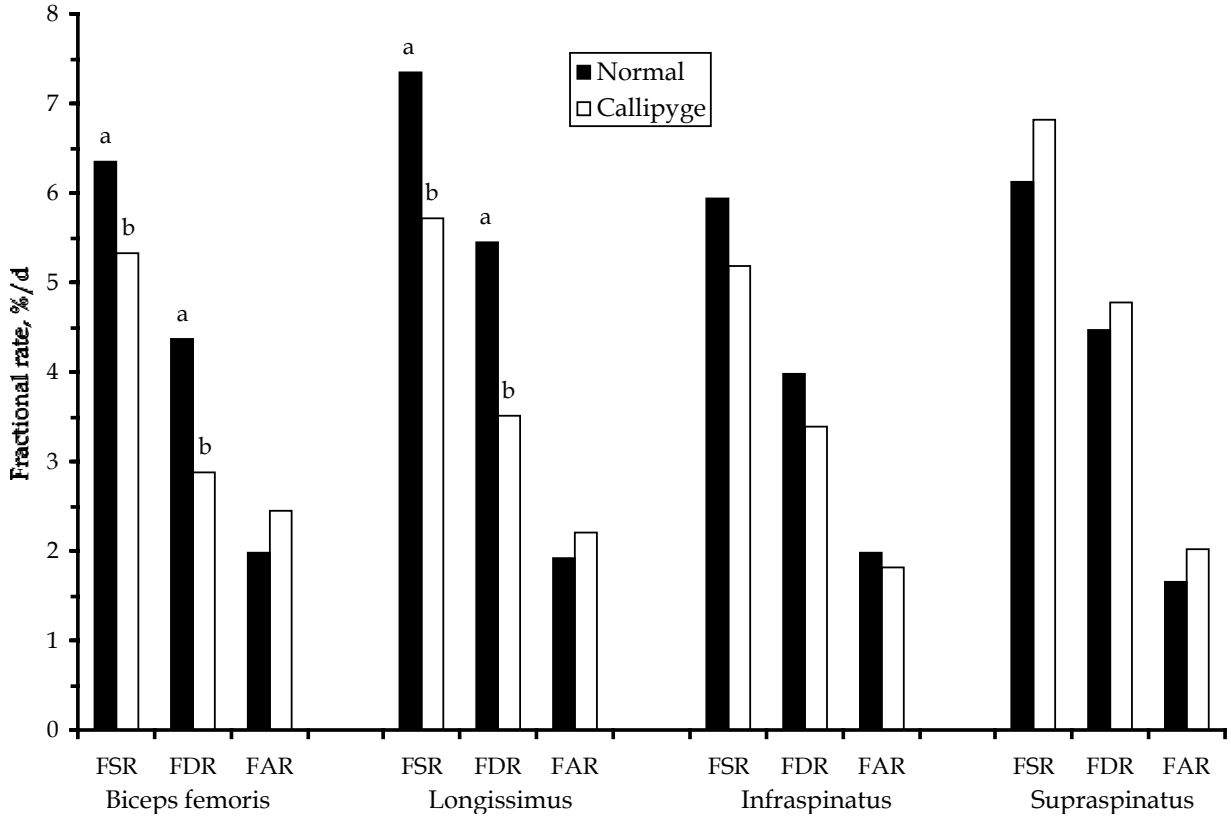

Figure 2. Effect of the callipyge phenotype on fractional rates of protein synthesis (FSR), degradation (FDR), and accretion (FAR) for both muscles that are hypertrophied by callipyge (biceps femoris and longissimus) and muscles that are not hypertrophied by callipyge (infraspinatus and supraspinatus). Adapted from Lorenzen et al. (1997).

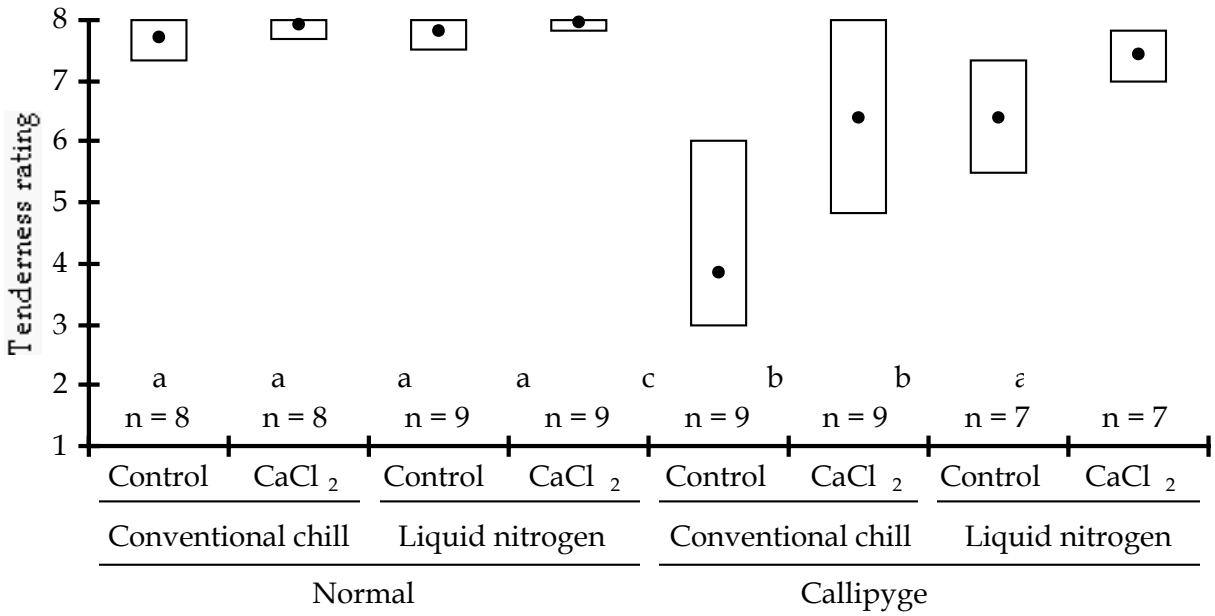

Figure 3. Effects of pre-rigor freezing of lamb carcasses with liquid nitrogen and post-rigor calcium chloride injection on sensory panel tenderness ratings of lamb at 14 d postmortem. Dots indicate the mean for each subclass. Horizontal bars indicate the range for each subclass. Letters above the x-axis indicate statistical differences; means not bearing a common superscript letter differ (SEM = .22; $P < .05$). Adapted from Koohmaraie et al. (1998).

Table 1. Effect of callipyge phenotype on yields.

Trait[a]	Normal	Callipyge	Change, %
Live weight, kg	52.2	52.8	1.1
Carcass weight, kg	26.6	29.2	9.8
Dressing percentage	51.0	55.3	8.5
--------Bone-in yields as a percentage of carcass weight ------			
Untrimmed	57.5	61.9	7.7
1/4" trimmed	54.4	59.9	10.1
Completely trimmed	50.3	55.7	10.7
---------Bone-in yields as a percentage of live weight --------			
Untrimmed	29.3	34.2	16.8
1/4" trimmed	27.7	33.1	19.5
Completely trimmed	25.6	30.8	20.2
-------Boneless yields as a percentage of carcass weight ------			
Completely trimmed	32.9	40.2	22.2
---------Boneless yields as a percentage of live weight -------			
Completely trimmed	16.8	22.2	32.6

[a]Adapted from Jackson et al. (1997b).

Table 2. Effect of the callipyge phenotype on muscle weights at various ages.

Muscle[a]	Age, d			
	28	84	169	775
	Change, %			
Biceps femoris	26.3**	34.0**	42.1**	45.8**
Semimembranosus	25.0**	37.5**	38.3**	47.5**
Longissimus	17.4**	23.7**	32.1**	43.9**
Gluteus group			31.0**	35.9**
Adductor	19.7**	28.8**	30.0**	37.4**
Semitendinosus	18.4**	10.7**	26.4**	33.1**
Psoas group			20.4**	29.0**
Quadriceps femoris			18.8**	13.9
Infraspinatus			6.9	4.6
Supraspinatus			2.9	-0.1

[a]Adapted from Koohmaraie et al. (1995) and Shackelford et al. (1998).

**$P < .01$.

Table 3. Effect of various tenderization methods on tenderness of broiled callipyge longissimus chops.

Experiment and treatment	Normal	Callipyge
Koohmaraie et al., 1995a		
1 d postmortem	7.5[b]	10.9[a]
7 d postmortem	4.7[c]	10.1[a]
21 d postmortem	3.3[d]	8.2[b]
Busboom et al., 1997		
14 d postmortem	3.8[c]	7.2[a]
80 d postmortem	3.3[d]	5.0[b]
Shackelford et al., 1998		
Posterior end of loin		
Not stimulated, 14 d postmortem	4.0[c]	5.5[b]
Electrically-stimulated, 14 d postmortem		6.0[b]
Anterior end of loin		
Not stimulated, 14 d postmortem	4.0[c]	7.3[a]
Electrically-stimulated, 14 d postmortem		6.0[b]
Koohmaraie et al., 1995b		
Not injected, 7 d postmortem	3.2[d]	9.5[a]
$CaCl_2$-injected, 7 d postmortem	3.0[d]	6.8[b]
Not injected, 21 d postmortem	3.2[d]	6.4[b]
$CaCl_2$-injected, 21 d postmortem	2.8[d]	4.5[c]
Leckie et al., 1997		
14 d postmortem	3.3	
$CaCl_2$-injected, 14 d postmortem		3.6
$CaCl_2$-injected, 28 d postmortem		3.1
Hydrodyne, 14 d postmortem		3.3

[abcd]Within an experiment, means that do not share a common superscript letter differ ($P > .05$).

Table 4. Comparison of the advantages and disadvantages of the lamb industry producing and marketing callipyge lamb with or without tenderization.

	Scenario[a]		
	Do not use callipyge	Use callipyge without tenderization	Use callipyge with tenderization
Breeder			
Added ram cost	0	-	-
Dystocia	0	0	0
Birth weight	0	0	0
Weaning weight	0	0	0
Lambs weaned/ewe	0	0	0
Feeder			
Feedlot rate of gain	0	0	0
Feed efficiency	0	+	+
Packer			
Dressing percentage	0	+	+
Cost of tenderization	0	0	-
Retailer			
Marketing options	0	0	?[b]
Cutting yield	0	++	++
Product attractiveness	0	++	++
Volume of lamb sold	0	?[c]	?[c]
Consumer			
Edible portion	0	++	++
Calories from fat	0	+	+
Tenderness	0	--	0[d]

[a]The number of "+" or "–" indicates the degree of favorable (+) or unfavorable (-) effect, and "0" indicates no effect.

[b]Depending on the method of tenderization chosen, product may not qualify for labeling as fresh lamb. Thus, marketing options may be reduced.

[c]It is unclear what the impact of callipyge meat would be on long-term sales volume.

[d]Depending on the method of tenderization chosen, product may still be tougher than normal lamb.

Table 5. Estimated effect of the callipyge phenotype on profitability of the lamb packing industry.

Item	Normal	Callipyge	Tenderized Callipyge
Live weight, pounds	115	115	115
Live cost, $/cwt	$90.00	$90.00	$90.00
Live cost, $	$103.50	$103.50	$103.50
Dressing percentage	51.0	55.3	55.3
Carcass weight, pounds	58.7	63.6	63.6
Three-way boxed lamb value, $/cwt	$188.00	$188.00	$188.00
Three-way boxed lamb value, $	$110.26	$119.56	$119.56
Tenderization cost	$0.00	$0.00	$5.00
Net Callipyge advantage, $		$9.30	$4.30

Table 6. Comparison of the genetic antagonisms associated with the callipyge phenotype in lamb and the intermediate and extreme double-muscled phenotypes in cattle.

	Phenotype[a]		
	Callipyge[a]	Intermediate double muscling[b]	Extreme double muscling[c]
Hyperplasia	0	+++	+++++
Hypertrophy	++++	+	+
Dystocia	0	+	+++++
Birth weight	0	+	++++
Weaning weight	0	?	?
Feedlot rate of gain	0	?	?
Feed efficiency	+	?	?
Dressing percentage	+	+	+++
Organ weights	+	+	++
Kidney-pelvic fat	+	+	++
Subcutaneous fat	+	+	++
Intermuscular fat	+	+	++
Intramuscular fat	++	+	++
Muscle:Bone	++	++	+++
Cutability	++	++	++++
Longissimus tenderness	--	0	0
Tenderness of muscles with high connective tissue content	-	0	++

[a]Assumes that the conventional scenario is that normal terminal line rams are mated to normal maternal line ewes and all offspring are slaughtered in a terminal crossing system. The number of "+" or "–" indicates the degree of favorable (+) or unfavorable (-) effect, and "0" indicates no effect of replacing the normal terminal line rams with homozygous callipyge terminal line rams.

[b]Assumes that the conventional scenario is that normal, terminal line bulls are mated to normal, mature (second parity or higher), maternal line cows and all offspring are slaughtered in a roto-terminal crossing system. The number of "+" or "–" indicates the degree of favorable (+) or unfavorable (-) effect, and "0" indicates no effect of replacing the normal terminal line bulls with homozygous double-muscled terminal line bulls.

[c]Assumes that the conventional scenario is that normal, terminal line bulls are mated to normal, mature (second parity or higher), maternal line cows and all offspring are slaughtered in a roto-terminal crossing system. The number of "+" or "–" indicates the degree of favorable (+) or unfavorable (-) effect, and "0" indicates no effect of replacing the normal terminal line bulls with homozygous double-muscled terminal line bulls and

replacing the normal maternal line cows with homozygous double-muscled cows.